Appendix 2: Benchmark simulations

In this appendix, we present a series of "benchmark" network simulations using both integrate-and-fire (IF) or Hodgkin-Huxley (HH) type neurons. They were chosen such that at least one of the benchmark can be implemented in the different simulators (the code corresponding to these implementations will be provided in the ModelDB database[39].

The models chosen were networks of excitatory and inhibitory neurons inspired from a recent study (Vogels and Abbott, 2005). This paper considered two types of networks of leaky IF neurons, one with current-based synaptic interactions (CUBA model), and another one with conductance-based synaptic interactions (CUBA model; see below). We also introduce here a HH-based version of the COBA model, as well as a fourth model consisting of IF neurons interacting through voltage deflections ("voltage-jump" synapses).

Network structure

Each model consisted of 4,000 IF neurons, which were separated into two populations of excitatory and inhibitory neurons, forming 80% and 20% of the neurons, respectively. All neurons were connected randomly using a connection probability of 2%.

Passive properties

The membrane equation of all models was given by:

$$C_m \frac{dV}{dt} = -g_L(V - E_L) + S(t) + G(t) , \tag{5}$$

where C_m = 1 μF/cm^2 is the specific capacitance, V is the membrane potential, g_L = 5×10^{-5} S/cm^2 is the leak conductance density and E_L = -60 mV is the leak reversal potential. Together with a cell area of 20,000 μm^2, these parameters give a resting membrane time constant of 20 ms and an input resistance at rest of 100 MΩ. The function $S(t)$ represents the spiking mechanism and $G(t)$ stands for synaptic interactions (see below).

Spiking mechanisms

IF neurons

In addition to passive membrane properties, IF neurons had a firing threshold of -50 mV. Once the Vm reaches threshold, a spike is emitted and the membrane potential is reset to -60 mV and remains at that value for a refractory period of 5 ms.

HH neurons

HH neurons were modified from Traub and Miles (1991) and were described by the following equations:

$$\begin{aligned}
C_m \frac{dV}{dt} &= -g_L(V - E_L) - \bar{g}_{Na}\, m^3 h\, (V - E_{Na}) - \bar{g}_{Kd}\, n^4\, (V - E_K) + G(t) \\
\frac{dm}{dt} &= \alpha_m(V)\,(1 - m) - \beta_m(V)\, m \\
\frac{dh}{dt} &= \alpha_h(V)\,(1 - h) - \beta_h(V)\, h \\
\frac{dn}{dt} &= \alpha_n(V)\,(1 - n) - \beta_n(V)\, n \,,
\end{aligned} \tag{6}$$

[39] http://senselab.med.yale.edu/senselab/ModelDB

where $\bar{g}_{Na} = 100\ mS/cm^2$ and $\bar{g}_{Kd} = 30\ mS/cm^2$ are the maximal conductances of the sodium current and delayed rectifier with reversal potentials of $E_{Na} = 50\ mV$ and $E_K = -90\ mV$. m, h, and n are the activation variables which time evolution depends on the voltage-dependent rate constants α_m, β_m, α_h, β_h, α_n and β_n. The voltage-dependent expressions of the rate constants were modified from the model described by Traub and Miles (1991):

$$
\begin{aligned}
\alpha_m &= 0.32 * (13 - V + V_T)/[\exp((13 - V + V_T)/4) - 1] \\
\beta_m &= 0.28 * (V - V_T - 40)/[\exp((V - V_T - 40)/5) - 1] \\
\alpha_h &= 0.128 * \exp((17 - V + V_T)/18) \\
\beta_h &= 4/[1 + \exp((40 - V + V_T)/5)] \\
\alpha_n &= 0.032 * (15 - V + V_T)/[\exp((15 - V + V_T)/5) - 1] \\
\beta_n &= 0.5 * \exp((10 - V + V_T)/40) \ ,
\end{aligned}
$$

where V_T = -63 mV adjusts the threshold (which was around -50 mV for the above parameters).

Synaptic interactions

Conductance-based synapses

For conductance-based synaptic interactions, the membrane equation of neuron i was given by:

$$C_m \frac{dV_i}{dt} = -g_L(V_i - E_L) + S(t) - \sum_j g_{ji}(t)(V_i - E_j) \ , \tag{7}$$

where V_i is the membrane potential of neuron i, $g_{ji}(t)$ is the synaptic conductance of the synapse from neuron j to neuron i, and E_j is the reversal potential of that synapse. E_j was of 0 mV for excitatory synapses, or -80 mV for inhibitory synapses.

Synaptic interactions were implemented as follows: when a spike occurred in neuron j, the synaptic conductance g_{ji} was instantaneously incremented by a quantum value (6 nS and 67 nS for excitatory and inhibitory synapses, respectively) and decayed exponentially with a time constant of 5 ms and 10 ms for excitation and inhibition, respectively.

Current-based synapses

For implementing current-based synaptic interactions, the following equation was used:

$$C_m \frac{dV_i}{dt} = -g_L(V_i - E_L) + S(t) - \sum_j g_{ji}(t)(\bar{V} - E_j) \ , \tag{8}$$

where $\bar{V}$ = -60 mV is the mean membrane potential. The conductance quanta were of 0.27 nS and 4.5 nS for excitatory and inhibitory synapses, respectively. The other parameters are the same as for conductance-based interactions.

Voltage-jump synapses

For implementing voltage-jump type of synaptic interactions, the membrane potential was abruptly increased by a value of 0.25 mV for each excitatory event, and it was decreased by 2.25 mV for each inhibitory event.

Benchmarks

Based on the above models, the following four benchmarks were implemented.

Benchmark 1: Conductance-based IF network. This benchmark consists of a network of IF neurons connected with conductance-based synapses, according to the parameters above. It is equivalent to the COBA model described in Vogels and Abbott (2005).

Benchmark 2: Current-based IF network. This second benchmark simulates a network of IF neurons connected with current-based synapses, which is equivalent to the CUBA model described in Vogels and Abbott (2005). It has the same parameters as above, except that every cell needs to be depolarized by about 10 mV, which was implemented by setting E_L = -49 mV (see Vogels and Abbott, 2005).

Benchmark 3: Conductance-based HH network. This benchmark is equivalent to Benchmark 1, except that the HH model was used.

Benchmark 4: IF network with voltage-jump synapses. This fourth benchmark used voltage-jump synapses, and has a membrane equation which is analytically solvable, and can be implemented using event-driven simulation strategies.

For all four benchmarks, the models simulate a self-sustained irregular state of activity, which is easy to identify: all cells fire irregularly and are characterized by important subthreshold voltage fluctuations. The neurons must be randomly stimulated during the first 50 ms in order to set the network in the active state.

Supplementary material

The supplementary material to the paper contains the codes for implementing those benchmarks in the different simulators reviewed here (see Section 3 for details on specific implementations). We provide the codes for those benchmarks, implemented in each simulator, and this code is made available in the ModelDB database[40].

In addition, we provide a clock-driven implementation of Benchmarks 1 and 2 with Scilab, a free vector-based scientific software. In this case, Benchmark 1 is integrated with Euler method, second order Runge-Kutta and Euler with spike timing interpolation (Hansel et al, 1998), while Benchmark 2 is integrated exactly (with spike timings aligned to the time grid). The event-driven implementation (Benchmark 4) is also possible with Scilab but very inefficient because the programming language is interpreted, and since the algorithms are asynchronous, the operations cannot be vectorized. Finally, we also provide a C++ implementation of Benchmark 2 and of a modified version of the COBA model (Benchmark 1, with identical synaptic time constants for excitation and inhibition).

[40] `http://senselab.med.yale.edu/senselab/ModelDB`